Critical mass of bacterial populations in a generalized Keller-Segel model. Analogy with the Chandrasekhar limiting mass of white dwarf stars

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(Dated: November 20, 2008)

We point out a remarkable analogy between the limiting mass of relativistic white dwarf stars (Chandrasekhar's limit) and the critical mass of bacterial populations in a generalized Keller-Segel model of chemotaxis [Chavanis & Sire, PRE, **69**, 016116 (2004)]. This model is based on generalized stochastic processes leading to the Tsallis statistics. The equilibrium states correspond to polytropic configurations similar to gaseous polytropes in astrophysics. For the critical index $n_3 = d/(d-2)$ (where $d \geq 2$ is the dimension of space), the theory of polytropes leads to a unique value of the mass M_c that we interpret as a limiting mass. In $d = 3$, we find $M_c = 202.8956...$ and in $d = 2$, we recover the well-known result $M_c = 8\pi$ (in suitable units). For $M < M_c$, the system evaporates (in an infinite domain) or tends to an equilibrium state (for box-confined configurations). For $M > M_c$, the system collapses and forms a Dirac peak containing a mass M_c surrounded by a halo. This paper exposes the model and shows, by simple considerations, the origin of the critical mass. A detailed description of the critical dynamics of the generalized Keller-Segel model will be given in a forthcoming paper.

Keywords: Chemotaxis; Generalized thermodynamics; Nonlinear meanfield Fokker-Planck equations; Self-gravitating Brownian particles

I. INTRODUCTION

Recently, there has been a growing interest for the dynamics and thermodynamics of systems with long-range interactions [1]. Such systems are numerous in Nature and share fascinating analogies. For example, the statistical mechanics of stellar systems (like globular clusters and elliptical galaxies) in astrophysics and the statistical mechanics of large-scale vortices (like Jupiter's great red spot) in two-dimensional turbulence present deep similarities [2] despite the very different physical nature of these systems. Some connections have also been developed between the dynamics of stellar systems and the dynamics of the Hamiltonian Mean Field (HMF) model [3, 4] and of the free electron laser [5]. More recently, the authors have studied a model of self-gravitating Brownian particles [6, 7, 8] and discovered striking analogies with the Bose-Einstein condensation in the canonical ensemble [9] and with the phenomenon of chemotaxis in biology [10]. In this paper, we point out a novel analogy between the Chandrasekhar limiting mass of white dwarf stars [11] and the critical mass of bacterial populations experiencing chemotactic aggregation.

The name chemotaxis refers to the motion of organisms induced by chemical signals [12]. In some cases, the biological organisms (bacteria, amoebae, endothelial cells, ants...) secrete a substance (pheromone, smell, food, ...) that has a long-range attractive effect on the organisms themselves. Therefore, in addition to their diffusive motion, they move preferentially along the gradient of concentration of the chemical they secrete (chemotactic flux). When attraction prevails over diffusion, the chemotaxis can trigger a self-accelerating process until a point at which aggregation takes place. This is the case for the slime mold *Dictyostelium discoideum* and for the bacteria *Escherichia coli*. This is referred to as chemotactic collapse. A model of slime mold aggregation has been introduced by Keller & Segel [13] in the form of two coupled differential equations. A simplified version of this model has been extensively studied in the case where the degradation of the secreted chemical can be neglected and an immediate production is assumed [14]. In that case, the Keller-Segel (KS) model become isomorphic to the Smoluchowski-Poisson (SP) system describing self-gravitating Brownian particles [7]. The steady states correspond to isothermal distributions similar to isothermal stars in astrophysics [15]. On the other hand, the KS model and the SP system can be viewed as standard mean field Fokker-Planck equations associated with the Boltzmann free energy [16, 17]. In this sense, they are based on ordinary thermodynamics. Since these systems are strongly dissipative, the correct statistical ensemble is the canonical ensemble [7].

Recently, modified forms of Keller-Segel models have been introduced in order to describe more general situations [18, 19, 20, 21, 22, 23, 24]. For example, in Ref. [20], we have introduced and studied a generalized Keller-Segel (GKS) model of chemotaxis taking into account anomalous diffusion. In this model, the coefficient of diffusion is assumed to depend on the density like $D(\rho) = D\rho^{\gamma-1}$ with $\gamma = 1 + 1/n$ (the ordinary KS model is recovered for $\gamma = 1$ or $n \to +\infty$). Anomalous diffusion is known to appear in many problems of biology [12] and it is likely that it can play a role in the process of chemotaxis. The generalized Keller-Segel (GKS) model is isomorphic to the generalized Smoluchowski-Poisson (GSP) system describing self-gravitating Langevin particles [20]. The steady states correspond to polytropic

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distributions similar to polytropic stars in astrophysics [15]. On the other hand, the GKS model and the GSP system can be viewed as nonlinear mean field Fokker-Planck equations [25, 26] associated with the Tsallis free energy [27]. In this sense, they are related to a notion of (effective) generalized thermodynamics.

For the GKS model, there exists a particular polytropic index $n_3 = d/(d-2)$ (where $d \geq 2$ is the dimension of space) at which the dynamics is critical. For this index, the theory of polytropes leads to a unique value of the mass M_c, independent on the size of the object, that we interpret as a limiting mass. This is the counterpart of the Chandrasekhar limiting mass [11] for white dwarf stars which are equivalent, in the ultra-relativistic limit, to polytropes of index $n = 3$ (in $d = 3$). This unexpected analogy between two systems that have apparently nothing in common was pointed out in [28] and is here systematically developed (see also Ref. [29]).

In this paper, we expose the GKS model (using the notations of biology) and show its relation to Tsallis generalized thermodynamics. Then, we show by simple considerations, the origin of the critical mass M_c appearing at the polytropic index $n_3 = d/(d-2)$. For $d = 3$, we find that $M_c = 202.89561...$ in a proper system of units. For $d = 2$ where $n_3 \to +\infty$, we recover the critical mass $M_c = 8\pi$ corresponding to the ordinary KS model in two dimensions whose critical dynamics has been extensively studied in [7, 8, 10] (see [30, 31, 32, 33, 34, 35, 36] for many rigorous results obtained by applied mathematicians). For $d = 3$, a detailed description of the critical dynamics of the GKS model for $M < M_c$ and $M > M_c$ in bounded and unbounded domains will be given in a forthcoming paper [29].

II. THE ORDINARY KELLER-SEGEL MODEL: BOLTZMANN THERMODYNAMICS

The primitive Keller-Segel model [13] describing the chemotaxis of bacterial populations [56] consists in two coupled differential equations

$$\frac{\partial \rho}{\partial t} = \nabla \cdot (D_2 \nabla \rho) - \nabla \cdot (D_1 \nabla c)\,, \tag{1}$$

$$\frac{\partial c}{\partial t} = D_c \Delta c + h(c)\rho - k(c)c, \tag{2}$$

which govern the evolution of the density of bacteria $\rho(\mathbf{r}, t)$ and the evolution of the secreted chemical $c(\mathbf{r}, t)$. The bacteria diffuse with a diffusion coefficient D_2 and they also move in a direction of a positive gradient of the chemical (chemotactic drift). The coefficient D_1 is a measure of the strength of the influence of the chemical gradient on the flow of bacteria. On the other hand, the chemical is produced by the bacteria with a rate $h(c)$ and is degraded with a rate $k(c)$. It also diffuses with a diffusion coefficient D_c. In the general Keller-Segel model, $D_1 = D_1(\rho, c)$ and $D_2 = D_2(\rho, c)$ can both depend on the concentration of the bacteria and of the chemical. This can take into account microscopic constraints, like close-packing effects or anomalous diffusion [24].

A simplified version of the Keller-Segel model is provided by the system of equations

$$\frac{\partial \rho}{\partial t} = \nabla \cdot (D \nabla \rho - \chi \rho \nabla c)\,, \tag{3}$$

$$\frac{\partial c}{\partial t} = D_c \Delta c + h\rho - kc, \tag{4}$$

where the parameters are positive constants. Another simplification is obtained in a limit of large diffusivity of the chemical $D_c \to +\infty$ and for sufficiently large concentrations of the bacteria (see [14] and Appendix C of [24] for details). In that case, Eq. (4) is replaced by a Poisson equation

$$\Delta c = -\lambda \rho, \tag{5}$$

where $\lambda = h/D_c$. Equation (3) can be viewed as a mean-field Fokker-Planck equation associated with a Langevin dynamics of the form

$$\frac{d\mathbf{r}}{dt} = \chi \nabla c + \sqrt{2D}\mathbf{R}(t), \tag{6}$$

where $\mathbf{R}(t)$ is a white noise, D is a diffusion coefficient and χ plays the role of a mobility. The Langevin equation describes a point organism performing a random walk biased in the direction of a drift velocity proportional to the local chemical gradient.

The KS model (3)-(5) monotonically decreases the Lyapunov functional

$$F = -\frac{1}{2}\int \rho c\, d\mathbf{r} + \frac{D}{\chi}\int \rho \ln \rho\, d\mathbf{r}, \tag{7}$$

which is similar to a free energy $F = E - T_{eff} S$ where $E = -(1/2)\int \rho c d\mathbf{r}$ is the energy of interaction and $S = -\int \rho \ln \rho d\mathbf{r}$ is the Boltzmann entropic functional. We have defined an effective temperature

$$T_{eff} = \frac{D}{\chi}, \tag{8}$$

which is given by a form of Einstein's formula. Using the KS model, we find that

$$\dot{F} = -\int \frac{1}{\chi\rho}(D\nabla\rho - \chi\rho\nabla c)^2 d\mathbf{r} \leq 0, \tag{9}$$

which is similar to the proper version of the H-theorem in the canonical ensemble [17, 25]. The stationary solutions of Eq. (3), corresponding to $\dot{F} = 0$, are given by

$$\rho = A e^{\frac{\chi}{D}c}, \tag{10}$$

where A is determined by the mass M. This is similar to the Boltzmann distribution for a system in a potential

$-c(\mathbf{r})$ at temperature $T_{eff}=D/\chi$. The steady states of Eq. (3) are critical points of the free energy F at fixed mass M. They cancel the first order variations $\delta F-\alpha\delta M=0$ where α is a Lagrange multiplier. Moreover, it can be shown [25] that they are linearly dynamically stable for the KS model if and only if they are (local) *minima* of F at fixed mass. The equilibrium state is obtained by coupling Eq. (10) to Eq. (5) leading to the Boltzmann-Poisson equation.

These analogies with thermodynamics take even more sense if we remark that the Keller-Segel model is isomorphic to the Smoluchowski-Poisson system

$$\frac{\partial\rho}{\partial t}=\nabla\cdot\left[\frac{1}{\xi}\left(\frac{k_BT}{m}\nabla\rho+\rho\nabla\Phi\right)\right], \tag{11}$$

$$\Delta\Phi=S_dG\rho, \tag{12}$$

describing the dynamics of self-gravitating Brownian particles in an overdamped limit and in a mean field approximation [6, 17]. We have the correspondence

$$D=k_BT/\xi m,\quad \chi=1/\xi,\quad c=-\Phi,\quad \lambda=S_dG. \tag{13}$$

We note, in particular, that the role of the gravitational potential Φ in the SP system is played, in the KS model, by the concentration $-c$ of the chemical. Therefore, the pheromonal substance has a long-range attractive effect similar to the gravitational attraction in astrophysics. In biology, the chemotactic aggregation is mediated by a physical field (the chemical produced by the organisms) while the nature of the gravitational force in astrophysics is more abstract. The equilibrium states of the SP system correspond to a condition of hydrostatic balance

$$\nabla P+\rho\nabla\Phi=\mathbf{0},\qquad \Delta\Phi=S_dG\rho, \tag{14}$$

with an isothermal equation of state

$$P=\rho k_BT/m. \tag{15}$$

Therefore, the equilibrium states of the KS model and SP system have the same structure as isothermal stars in astrophysics [15]. Of course, the dynamics of the KS model and SP system is different from the dynamics of stars which is rather described by hydrodynamic equations like the Euler-Poisson system [37].

III. THE GENERALIZED KELLER-SEGEL MODEL: TSALLIS THERMODYNAMICS

In a previous paper [20] (see also [23]), we have introduced and studied a generalized Keller-Segel model of the form

$$\frac{\partial\rho}{\partial t}=\nabla\cdot\left(D\nabla\rho^\gamma-\chi\rho\nabla c\right), \tag{16}$$

$$\Delta c=-\lambda\rho. \tag{17}$$

Comparing with the primitive Keller-Segel model (1)-(2), it corresponds to $D_2=D\gamma\rho^{\gamma-1}$ and $D_1=\chi\rho$. For simplicity, we have considered that the chemical is determined by a Poisson equation (17). More generally, we can consider that it satisfies the field equation (4). However, the analytical results that we obtain in Secs. IV and V are only valid for the Poisson equation (17). For $\gamma=1$, we recover the ordinary Keller-Segel model (3)-(5). Equation (16) can be viewed as a nonlinear mean field Fokker-Planck equation of the form considered in [25, 26, 38, 39]. It can be obtained from the stochastic process

$$\frac{d\mathbf{r}}{dt}=\chi\nabla c+\sqrt{2D}\rho^{(\gamma-1)/2}\mathbf{R}(t), \tag{18}$$

where $\mathbf{R}(t)$ is a white noise [57]. This equation describes a situation where the mobility χ is constant but the diffusion coefficient $D(\rho)=D\rho^{\gamma-1}$ can depend on the density. This can account for anomalous diffusion and nonergodic behaviors. For $\gamma=1$, we recover the ordinary Langevin equation (6) with constant diffusion coefficient D and constant mobility χ. The stochastic process (18) has been introduced by Borland [42] in relation with Tsallis generalized thermodynamics [27]. For $\gamma=1$, we have a pure random walk. In that case the sizes of the random kicks are uniform and do not depend on where the particle happens to be. For $\gamma\neq 1$, the size of the random kicks changes, depending on the distribution of the particles around the "test" particle. A particle which is in a region that is weakly populated [small $\rho(\mathbf{r},t)$] will tend to have smaller kicks if $\gamma>1$ and larger kicks if $\gamma<1$. Since the microscopics depends on the actual density, this creates a bias in the ergodic behavior of the system.

The GKS model decreases the Lyapunov functional

$$F=-\frac{1}{2}\int\rho c d\mathbf{r}+\frac{D}{\chi}\frac{1}{\gamma-1}\int(\rho^\gamma-\rho)d\mathbf{r}. \tag{19}$$

It can be interpreted as a generalized free energy of the form $F=E-T_{eff}S$ where $E=-(1/2)\int\rho c d\mathbf{r}$ is the energy and $S=-1/(\gamma-1)\int(\rho^\gamma-\rho)d\mathbf{r}$ is the Tsallis entropy (the polytropic index γ plays the role of the Tsallis q parameter). The effective temperature T_{eff} is still given by the Einstein-like formula (8). Using the GKS model, we find that

$$\dot{F}=-\int\frac{1}{\chi\rho}(D\nabla\rho^\gamma-\chi\rho\nabla c)^2d\mathbf{r}\leq 0, \tag{20}$$

which is similar to the proper version of the H-theorem in the canonical ensemble in a generalized thermodynamical framework [17, 25]. The stationary solution of Eq. (16), corresponding to $\dot{F}=0$, is given by

$$\rho=\left[\mu+\frac{\chi}{D}\frac{\gamma-1}{\gamma}c\right]^{1/(\gamma-1)}, \tag{21}$$

where μ is determined by the mass M. This corresponds to the Tsallis distribution with inverse temperature $\beta=$

$1/T_{eff} = \chi/D$ and "q-parameter" γ. The steady states of Eq. (16) are critical points of the free energy F at fixed mass M. They cancel the first order variations $\delta F - \alpha\delta M = 0$ where α is a Lagrange multiplier. Moreover, it can be shown that they are linearly dynamically stable for the GKS model if and only if they are (local) *minima* of F at fixed mass [25]. The equilibrium state is obtained by coupling Eq. (21) to Eq. (17) leading to the "Tsallis-Poisson" equation.

These analogies with generalized thermodynamics take even more sense if we remark that the GKS model is isomorphic to the generalized Smoluchowski-Poisson system [20]:

$$\frac{\partial\rho}{\partial t} = \nabla\cdot\left[\frac{1}{\xi}\left(K\nabla\rho^\gamma + \rho\nabla\Phi\right)\right], \tag{22}$$

$$\Delta\Phi = S_d G\rho, \tag{23}$$

provided that we set

$$D = K/\xi, \quad \chi = 1/\xi, \quad c = -\Phi, \quad \lambda = S_d G. \tag{24}$$

In particular, the equilibrium states correspond to a condition of hydrostatic balance

$$\nabla P + \rho\nabla\Phi = \mathbf{0}, \qquad \Delta\Phi = S_d G\rho, \tag{25}$$

with a polytropic equation of state

$$P = K\rho^\gamma. \tag{26}$$

Therefore, the equilibrium states of the GKS model and GSP system have the same structure as polytropic stars in astrophysics [15]. As in astrophysics, we define the polytropic index n by

$$\gamma = 1 + \frac{1}{n}. \tag{27}$$

IV. THE CRITICAL MASS OF BACTERIAL POPULATIONS FOR $n = n_3$

The steady states of the GKS model are determined by substituting the polytropic distribution (21) in the Poisson equation (17). The resulting configurations have the same structure as polytropic stars in astrophysics. Therefore, we can readily apply the theory of polytropes developed long ago by Emden [43] to the biological problem. For sake of generality, we extend these results to a space of d dimensions [20]. The dimension $d = 2$ (which is important in biology) will be considered specifically in Sec. V.

We consider spherically symmetric configurations. Defining

$$\rho = \rho_0\theta^n, \qquad \xi = \left[\frac{\lambda\chi\rho_0^{1-1/n}}{D(1+n)}\right]^{1/2} r, \tag{28}$$

where ρ_0 is the central density, and using the Poisson equation (17) with the steady distribution (21), we find after simple algebra that the function $\theta(\xi)$ is solution of the Lane-Emden equation

$$\frac{1}{\xi^{d-1}}\frac{d}{d\xi}\left(\xi^{d-1}\frac{d\theta}{d\xi}\right) = -\theta^n, \tag{29}$$

with $\theta = 1$ and $\theta' = 0$ at $\xi = 0$. In the following, we consider $d > 2$ and $n > 0$. It is shown in [20] that polytropic configurations are self-confined iff

$$n < n_5 = \frac{d+2}{d-2}. \tag{30}$$

In that case, the function $\theta(\xi)$ vanishes at a finite distance $\xi = \xi_1$. Consequently, the density $\rho(r)$ vanishes at a distance R_* defining the radius R_* of the polytrope. The relation between the radius and the central density is

$$\xi_1 = \left[\frac{\lambda\chi\rho_0^{1-1/n}}{D(1+n)}\right]^{1/2} R_*. \tag{31}$$

The mass $M = \int_0^{R_*}\rho S_d r^{d-1}dr$ of the configuration is given by

$$M = S_d\rho_0\left[\frac{D(1+n)}{\lambda\chi\rho_0^{1-1/n}}\right]^{d/2}\int_0^{\xi_1}\theta^n\xi^{d-1}d\xi. \tag{32}$$

Using the Lane-Emden equation (29), we get

$$M = -S_d\rho_0\left[\frac{D(1+n)}{\lambda\chi\rho_0^{1-1/n}}\right]^{d/2}\xi_1^{d-1}\theta_1'. \tag{33}$$

Expressing the central density in terms of the radius, using Eq. (31), and introducing the index

$$n_3 = \frac{d}{d-2}, \tag{34}$$

we obtain the mass-radius relation

$$M^{(n-1)/n}R_*^{[(d-2)(n_3-n)]/n} = \frac{D(1+n)}{\lambda\chi S_d^{(1-n)/n}}\omega_n^{(n-1)/n}, \tag{35}$$

where

$$\omega_n = -\xi_1^{(n+1)/(n-1)}\theta_1'. \tag{36}$$

This is nothing but the usual mass-radius relation for polytropes [43] extended to d dimensions [20], and written with the notations of biology.

For $n < n_3$ there is one, and only one, steady state for each mass M and it is stable (global minimum of $F[\rho]$ at fixed mass M). Its radius R_* is determined by Eq. (35). For $n_5 > n > n_3$ there is one, and only one, steady state for each mass M but it is unstable (saddle point of $F[\rho]$

at fixed mass). The index n_3 is *critical* [20]. For $n = n_3$, steady state solutions exist for a unique value of the mass

$$M_c = S_d \left[\frac{D(1+n_3)}{\lambda\chi}\right]^{n_3/(n_3-1)} \omega_{n_3}. \quad (37)$$

Their radius R_* is arbitrary and they are marginally stable. This yields a family of density profiles of the form

$$\rho(r) = \rho_0 \theta^{n_3}(\xi_1 r/R_*), \quad (38)$$

where ρ_0 is related to R_* by Eq. (31). They all have the same mass (37) and it can be shown that their free energy is independent of R_* (see Appendix F of [20]). The invariant profile $\theta(\xi)^{n_3}$ is plotted in Fig. 1. In $d = 3$ where $n_3 = 3$, the critical mass is

$$M_c = 32\pi\omega_3 \left(\frac{D}{\lambda\chi}\right)^{3/2}. \quad (39)$$

It is found by solving numerically the Lane-Emden equation that $\omega_3 = 2.01824...$ [15]. Therefore, we obtain more quantitatively

$$M_c = 202.8956... \left(\frac{D}{\lambda\chi}\right)^{3/2}. \quad (40)$$

It can be convenient to introduce dimensionless variables or, equivalently, to take $D = \lambda = \chi = 1$. In that case, the only control parameter is the mass M. With this system of units, the critical mass in $d = 3$ is $M_c = 202.8956....$

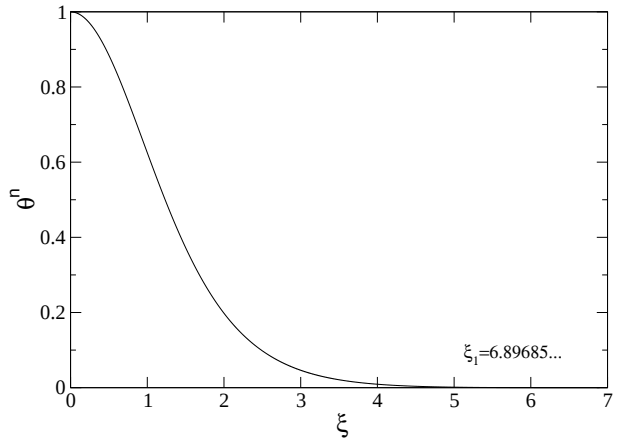

FIG. 1: Invariant density profile for the 3D generalized Keller-Segel model at the critical index $n = 3$ and critical mass M_c.

The critical mass (39) of bacterial populations is the counterpart of the Chandrasekhar limiting mass for white dwarf stars [11]. The analogy stems from the fact that, in the ultra-relativistic limit, white dwarf stars are equivalent to polytropes with the critical index $n = 3$ (in $d = 3$). Then, applying the theory of polytropes, Chandrasekhar [11] obtains a unique value of the mass

$$M_{Chandra} = \left(\frac{3}{32\pi^2}\right)^{1/2} \omega_3 \left(\frac{hc}{G}\right)^{3/2} \frac{1}{(\mu H)^2}, \quad (41)$$

where h is the Planck constant, c is the velocity of light, G is the constant of gravity and H is the mass of the hydrogen atom (μ is the molecular weight). In terms of the solar mass, it reads

$$M_{Chandra} = 0.196701... \left(\frac{hc}{G}\right)^{3/2} \frac{1}{(\mu H)^2} \simeq 5.76 M_\odot/\mu^2. \quad (42)$$

In his more general treatment of partially relativistic white dwarf stars, Chandrasekhar [44] shows that the mass (42) represents a limit above which there is no equilibrium state [58]. In that case, the system is expected to collapse leading ultimately to a neutron star or a black hole.

V. THE TWO-DIMENSIONAL CASE

In two dimensions ($d = 2$), the critical polytropic index $n_3 \to +\infty$. In that case, $\gamma = 1$ and we recover the usual Keller-Segel model (3)-(5) corresponding to normal diffusion. The stationary solution is obtained by substituting the Boltzmann distribution (10) in the Poisson equation (5). The resulting configurations have the same structure as isothermal stars in astrophysics. Their structure in d dimensions has been described in [7].

We consider spherically symmetric configurations. Defining

$$\rho = \rho_0 e^{-\psi}, \qquad \xi = (\lambda\chi\rho_0/D)^{1/2} r, \quad (43)$$

where ρ_0 is the central density, we find after simple algebra that ψ is solution of the Emden equation

$$\frac{1}{\xi^{d-1}} \frac{d}{d\xi}\left(\xi^{d-1}\frac{d\psi}{d\xi}\right) = e^{-\psi}, \quad (44)$$

with $\psi = 0$ and $\psi' = 0$ at $\xi = 0$. For $d = 2$, the density profile extends to infinity but the total mass is finite. The mass $M = 2\pi \int_0^{+\infty} \rho r dr$ is given by

$$M = \frac{2\pi D}{\chi\lambda} \int_0^{+\infty} e^{-\psi} \xi d\xi. \quad (45)$$

Using the Emden equation (44), we get

$$M = \frac{2\pi D}{\chi\lambda} \lim_{\xi\to+\infty} \xi\psi'(\xi). \quad (46)$$

In $d = 2$, the Emden function is known analytically [7]:

$$e^{-\psi} = \frac{1}{\left(1 + \frac{1}{8}\xi^2\right)^2}, \quad (47)$$

and we find that $\xi\psi' \to 4$ for $\xi \to +\infty$. This leads to a unique value of the mass

$$M_c = \frac{8\pi D}{\chi\lambda}. \quad (48)$$

Therefore, unbounded steady states of the KS model in two dimensions exist for a unique value of the mass (48) and they are marginally stable [10]. This yields a family of density profiles of the form

$$\rho(r) = \frac{\rho_0}{\left(1+\frac{\lambda\chi\rho_0}{8D}r^2\right)^2}, \tag{49}$$

that are parametrized by the central density ρ_0. They all have the same mass (48) and it can be shown that their free energy is independent of ρ_0 [10]. The invariant profile $e^{-\psi(\xi)}$ is plotted in Fig. 2.

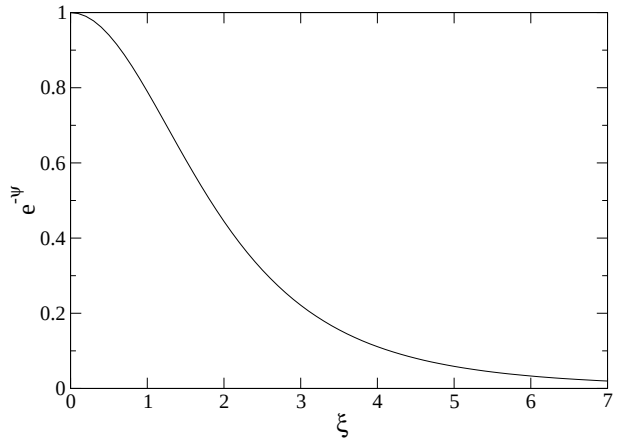

FIG. 2: Invariant density profile for the two-dimensional Keller-Segel model at the critical mass M_c.

The critical mass of bacterial populations (48) is the counterpart of the critical mass or critical temperature

$$M_c = \frac{4k_BT}{Gm}, \qquad k_BT_c = \frac{GMm}{4}, \tag{50}$$

of isothermal spheres in 2D gravity (see Ref. [10] for a description of this analogy). The existence of a critical mass, or critical temperature, for systems described by the 2D Boltzmann-Poisson system is known for a very long time in astrophysics [7, 45, 46, 47, 48, 49, 50, 51, 52] and in the statistical mechanics of 2D point vortices [2, 53, 54, 55]. It has been rediscovered in the context of chemotaxis in [10, 30, 31, 32, 33, 34, 35, 36]. Comparing Eq. (46) with Eq. (33) we find that for $d = 2$ and $n = n_3 \to +\infty$, we have the limit

$$\lim_{d\to 2} n_3\omega_{n_3} = 4. \tag{51}$$

This relation can also be obtained from Eq. (79) in [20]. With this relation (51), we can obtain the critical mass (48) of the KS model in two dimensions as a particular case of the critical mass (37) of the GKS model when $d \to 2$. In the context of generalized thermodynamics, this corresponds to the limit $\gamma \to 1$ where we pass from the Tsallis (polytrope) distribution to the Boltzmann (isothermal) distribution. In the present context, this corresponds to the passage from anomalous ($\gamma > 1$) to normal ($\gamma = 1$) diffusion.

VI. CONCLUSION

Our study tends to suggest that a notion of generalized thermodynamics can be useful in the context of chemotaxis when the biological organisms experience anomalous diffusion. Therefore, the chemotactic aggregation of bacterial populations could be an important *physical* system where ideas of generalized thermodynamics apply. The generalized Keller-Segel model (16)-(17) that we have introduced is related to the Tsallis form of entropic functional. This is a very rich model because *it combines both elements of generalized thermodynamics and long-range interactions*. Therefore, it enters in the general class of nonlinear mean field Fokker-Planck equations introduced by Chavanis [25]. In fact, we can develop an effective generalized formalism for an even larger class of entropic functionals than the Tsallis entropy. For example, we can consider a generalized stochastic process

$$\frac{d\mathbf{r}}{dt} = \chi\nabla c + \sqrt{\frac{2\chi P(\rho)}{\rho}}\mathbf{R}(t), \tag{52}$$

where the diffusion coefficient is given by $D(\rho) = \chi P(\rho)/\rho$ where $P(\rho)$ is an almost arbitrary function which plays the role of an equation of state in the analogy with barotropic stars in astrophysics [20]. Then, we get the GKS model

$$\frac{\partial\rho}{\partial t} = \nabla\cdot\left[\chi\left(\nabla P - \rho\nabla c\right)\right], \tag{53}$$

$$\Delta c = -\lambda\rho. \tag{54}$$

The equilibrium states correspond to the condition of hydrostatic equilibrium (14). This system satisfies a formalism of generalized thermodynamics [24] for a class of entropic functionals

$$F = -\frac{1}{2}\int \rho c d\mathbf{r} + \int \rho \int^{\rho} \frac{P(\rho')}{\rho'^2} d\rho' d\mathbf{r}, \tag{55}$$

larger than the Tsallis entropic functional [59]. However, the Tsallis thermodynamics is convenient to describe deviations from the Boltzmann thermodynamics in a simple manner. This leads to models that are still analytically tractable. For example, the GKS model (16)-(17) can be studied in great detail [20, 23, 29].

For the index n_3, the GKS model (16)-(17) presents a critical dynamics involving a "universal" mass M_c *independent on the size of the system*. In astrophysics, this result is well-known in $d = 3$ and is connected to the limiting mass of white dwarf stars discovered by Chandrasekhar [11]. We can immediately transpose this result to the biological context leading to the critical mass (40) of bacterial populations. This result was implicit in [20] and it has been developed in the present paper with emphasis. Thus, our paper reveals the analogy of the existence of a critical mass, found initially for white

dwarf stars, to exist also for bacterial populations driven by chemotaxis. Now, the question concerns the detailed description of the critical dynamics of the GKS model at $n = n_3$. This will be reported in a forthcoming paper [29]. From the present study, we anticipate that the critical dynamics of the GKS model at $n_3 = 3$ in $d = 3$ will be very similar to the critical dynamics of the ordinary KS model with $n_3 = +\infty$ in $d = 2$ studied in [7, 8, 10]. This analogy will be confirmed in [29]. For $M < M_c$, we find that the system evaporates (in an infinite domain) or tends to an equilibrium state (in a finite domain) corresponding to an *incomplete polytrope* confined by the box. For $M > M_c$, we find that the system collapses. In a finite time, it forms a Dirac peak containing a mass M_c surrounded by a halo that has a pseudo self-similar evolution. These results are similar to those found in $d = 2$. In conclusion, we can interpret the mass M_c as *a limiting mass above which the system undergoes chemotactic collapse*. This strengthens the analogy with the Chandrasekhar mass of white dwarf stars. There is, however, a great conceptual difference between the two. Indeed, the Chandrasekhar mass is defined in terms of fundamental constants so it has a universal value. By contrast, the critical mass of bacterial populations depends on the parameters λ, χ and D that are not universal and that change from experiment to experiment. Furthermore, the index $n = 3$ in $d = 3$ is special in astrophysics because it corresponds to the index of ultra-relativistic and completely degenerate white dwarf stars [15]. In biology, there is *a priori* no reason why the index $n = n_3$ should be selected in the dynamics of bacterial populations (except in $d = 2$ where it corresponds to a situation of ordinary diffusion).

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[56] To be specific, we assume that the biological organisms experiencing chemotaxis are bacteria, but our results can be valid for other systems like amoebae, cells, social insects... The Keller-Segel model generically describes a wide variety of biological systems.

[57] There are other methods to justify the GKS model (16)-(17). It can be obtained from the master equation, assuming that the probabilities of transition explicitly depend on the occupation number (concentration) of the initial and arrival states [22, 40]. It can also be obtained in a strong friction limit of a generalized kinetic model taking into account inertial effects [24, 41].

[58] The structure and the stability of (relativistic) white dwarf stars in d dimensions has been studied in [28]. It is found that the dimension $d = 3$ of our universe plays a very particular (marginal) role.

[59] Note that the model (53)-(54) is still a particular case of the primitive Keller-Segel model (1)-(2). However, the primitive Keller-Segel model does not satisfy a formalism of generalized thermodynamics. Apparently, the most general form of Keller-Segel model satisfying a formalism of effective generalized thermodynamics (effective temperature, Einstein's relation, H-theorem,...) is provided by Eqs. (134)-(135) of [24].